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COMPARATIVE ANATOMY

OF THE

BARKS OF THE SALICACEÆ

(PART I.)

BY

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Introductory.

In a paper presented to this Conference last year by Dr. H. A. D. Jowett and Mr. C. E. Potter, entitled "Variations in the Occurrence of Salicin and Salinigrin in Different Willow and Poplar Barks" ('Y.-B.P,' 1902, p. 483), they showed that differences of species were not the only factors to be considered in ascertaining the probable yield of glucoside by these barks. The factor of species, however, is one of considerable importance, as instanced, for example, by the fact that *Salix discolor* yields salinigrin instead of salicin, while manufacturers of the latter state that *S. viminalis* never yields any glucoside. It is well known that the accurate determination of species in the Salicaceæ, more especially in the willows, is at times a matter of great difficulty, even with complete herbarium specimens. The addition, if possible, of diagnostic characters gleaned from a study of the anatomy of their barks cannot fail, therefore, to be of some value. When we add to this the fact that the manufacturer or the pharmacist seldom has anything but the bark itself to guide him in its identification, the importance of such characters becomes manifest.

In view of the complexity and length of the study here undertaken, it has been found necessary to place some limitations on its treatment from the comparative standpoint. It will, therefore, be well to state at the outset that, in seeking for characters which may serve to differentiate the barks, that stage (with one exception) has been chosen in which the epidermis has been thrown off, but before internal periderms

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have begun to form. Furthermore, only transverse sections have been considered, although a large number of radial and tangential sections has been examined, in order to check the accuracy of the interpretation of transverse sections. In considering the general features of the group, I have also thought it desirable to record some observations on the younger stages, but in the detailed examination the limits set forth above have been adhered to.

General.

The observations hitherto recorded consist, for the most part, of structural descriptions of the barks of a few species (of *Salix* mostly) and of the histological details of portions (especially the epidermis and cork of the willows) of a larger number of them. For the comparative study of a more extensive series of barks we are indebted to von Höhnel, who examined eleven species of *Salix*, and to Moeller, who described four species of *Populus* and two of *Salix* in some detail, and upon them based an account of the anatomical features of the whole group. As frequent reference will be made to the statements of these various investigators, a list of such of their works as have been consulted is here appended :—

Dr. Franz R. von Höhnel, 'Die Gerberinden,' pp. 87-95. Berlin, 1880. Hereinafter referred to as "von Höhnel."

Dr. Joseph Moeller, 'Anatomie der Baumrinden,' pp. 89-95. Berlin, 1882. This contains citations of the earlier literature. Hereinafter referred to as "Moeller."

Dr. A. de Bary, 'Comparative Anatomy of the Phanerograms and Ferns.' Bower and Scott's translation. Oxford, 1884. Also contains citations of the earlier literature. Hereinafter referred to as "de Bary."

H. Douliot, "Recherches sur le Périderme," in *Annales des Sciences naturelles*, septième série, tome dixième, p. 330. Paris, 1889. Hereinafter referred to as "Douliot."

Dr. J. E. Weiss, "Beiträge zur Kenntnis der Korkbildung," in *Bayerischen Botanischen Gesellschaft zu Regensburg*, p. 52. Regensburg, 1890. Hereinafter referred to as "Weiss."

Hermann Ross, "Contribuzioni alla Conoscenza del Periderma," in *Malpighia*, Vol. IV., p. 104. Genova, 1890-91. Hereinafter referred to as "Ross."

MM. G. Planchon et E. Collin, 'Les Drogues Simples d'Origine Végétale,' tome premier, pp. 254-256. Paris, 1895. Hereinafter referred to as "Planchon and Collin."

Dr. Hans Solereder, 'Systematische Anatomie der Dicotyledonen,' p. 896-898. Stuttgart, 1899. Hereinafter referred to as "Solereder."

In the general description of the anatomical features of the barks of the Salicaceæ, the tissues will first be considered in crder, beginning at the periphery, and such of these features as are considered to be of importance in differentiating the two genera of which the order consists will then be enumerated.

(I) The Epidermis and the Tissues Derived from the Phellogen.

The epidermis, which will be only briefly referred to here, consists of small cells which are nearly cubical or slightly elongated tangentially in transverse section, and which possess thickened and cuticularised outer walls. Tangential elongation is, on the whole, more frequent in the poplars (*ep.*, Figs. 1, 2, 3, and 6) than in the willows (*ep.*, Figs. 10, 11, 13 and 14), whereas the thickening of the outer wall is, as a rule, more pronounced in the willows than in the poplars; the former, however, differ among themselves to some extent in this respect—compare, for instance, Fig. 10 (*S. alba*) with Figs. 11 (*S. Wardi*), and 13 or 14 (*S. viminalis*). The epidermis may be glabrous, or nearly so (*P. angustifolia, S. pentandra*), or it may be provided with hairs (*P. alba, S. Caprea*). It is interesting to note, in this connection, that the bud-scales of *P. Fremonti* possess hairs which are stained pink with phloroglucin and hydrochloric acid when cut or broken, but are unaffected by that reagent when intact.

The origin of the periderm has been repeatedly investigated by various workers in a number of species of *Populus* and *Salix*, and the main conclusions are satisfactorily established, but in matters of detail there are some discrepancies which will now be considered.

In *Salix* the periderm originates in the epidermis itself (Figs. 10, 13, and 14). No exceptions to this rule appear to have been recorded, and I have not observed any. With regard to the products of the activity of the phellogen, the same unanimity does not exist. According to de Bary (p. 549), each initial epidermal cell, in most investigated species of *Salix*, produces in the first year *one* cork cell externally, and *one* phellodermal cell internally; between the two there is a central meristematic cell, with its wall

thickened on the outside, and immediately becoming cuticularised on the external thickened surface. In this central meristematic cell the same division and differentiation as in the initial epidermal cell is repeated in the second year, and the same process takes place in each succeeding year, starting from the meristematic cell for the time being, until the formation of outer bark begins at a later period. Von Höhnel (p. 91) confirms the above as far as the configuration of the cork cells is concerned. Weiss also confirms this point, but in the six species of *Salix* (these include *S. Caprea* and *S. alba*) which he investigated he found that, almost without exception, a phelloderm cell was formed by the first tangential wall, and that, by the second and several succeeding ones, cork cells were cut off on the outer side. The observations of Ross coincide, on the whole, with those of de Bary, but he contends that it is the inner wall of the outermost cell resulting from the division of the initial epidermal cell (*i.e.*, the one which bears the cuticle externally) which becomes thickened, and not the outer wall of the central meristematic cell; and he emphasises his contention by stating that this is the only case known in which the suberised lamella is more strongly developed on the inner wall than on the other walls of a cell. He also introduces another slight variation in asserting that there may be two layers of periderm or cork ("phellem") formed annually. Moeller (p. 89) makes no reference to the presence of phelloderm, but confirms the formation of a single row of cork cells annually; he, however, specifically modifies the statement that the outer walls of each layer of cells become thickened, and holds that this may only occur at intervals, as instanced by *S. fragilis*. Finally, Douliot asserts that no phelloderm is formed (in *S. Caprea*)—during the first two years, at all events—and that the quantity of cork produced is dependent on the amount of illumination which the plant receives, being abundant in the light, but scanty in the shade. It would appear, further, that, of the rows of cork formed during the course of one year, only the last formed becomes thickened in the external portion of its cells.

My own observations, which are still incomplete, but which I hope to supplement in Part II., dealing more particularly with the willows, would lead me to conclude that, in the large majority of cases, the observations recorded by de Bary (waiving, for the present, the rather fine issue raised by Ross as to the localisation of the region of thickening) hold good,

with the exception, perhaps, of the amount of phelloderm formed annually. It is only fair to state, however, that the observations which I have so far been able to make on the amount of phelloderm formed annually are hardly sufficient to justify an expression of opinion one way or the other, inasmuch as these phelloderm cells are subject to tangential elongation soon after they are formed, and ultimately become excessively drawn out, so that any indication of their mode of origin is entirely obliterated. The exceptions to the rule that a phelloderm cell is formed by the first tangential wall do not seem to be so rare as Weiss has supposed (see Figs. 13 and 14), but this will be discussed later. The presence of intervening rows of thin-walled cork cells between those which have thickened outer walls appears, on the other hand, to be an exceptional feature; the examples of it which I have had under my own observation occur locally, a fact which would seem to lend support to Douliot's conclusions. But in the one case of *S. Wardi* the exception becomes the rule (Fig. 11), and in the second year the formation of internal periderms begins (Fig. 9), these frequently going so far as to enclose groups of the pericyclic fibres. The outer bark in this instance (*k*, Fig. 9) includes many layers of thin-walled cells which are manifestly due to the activity of a phellogen.

From what has been said above it will be seen that the thickened cells of the periderm form a characteristic feature of the willow barks. Their thickened outer walls bulge outwards, presenting a convex surface externally and a concave one internally—especially well seen in a radial section: they are always suberised, but not lignified. The following differences in the characters exhibited by the cells of the periderm of different species appear to be of diagnostic value:—

(1) Size of the cells, especially as measured in a tangential direction. Thus, the cells of the periderm in the bark of *S. fluviatilis* are much more delicate than those of *S. purpurea* (Fig. 12), and seldom attain more than half the size of the latter in a tangential direction.

(2) Amount of thickening which the outer walls undergo. Thus, in *S. viminalis* (Fig. 15) and *S. triandra* these walls are relatively thin, while in *S. purpurea* (Fig. 12) and in the majority of willows they are much thicker.

(3) The shape of the thickenings. Thus, in *S. missouriensis* and *S. viridis* (compare, also, Fig. 12) the outer surface is usually verrucose or mammillated, while in *S. nigra* and *S. viminalis* (Fig. 15) it is nearly even. It must be remem-

bered, however, that the walls in the outer rows may become more or less straightened out by tangential extension. The factor considered below is undoubtedly of some importance also in this connection.

(4) The number of cork cells adhering to the bark. This factor, as one would expect, is subject to considerable variation, but the striking contrast of a case like *S. viridis*, which sometimes exhibits as many as seven rows of adherent cork cells, with *S. nigra*, which rarely possesses more than two rows, cannot fail to be of some value. The causes which appear to underlie this factor of adherence or non-adherence of the periderm layers are of great interest, but a discussion of them at this stage would take us beyond the limits of this part of the subject; they will accordingly be treated of in Part II.

The colour of the cork membranes is, according to de Bary (p. 112), distinctive also, these being colourless in some species (*S. viminalis*, *S. aurita*, and *S. Caprea*) and yellow in others (*S. alba*, *S. purpurea*, and *S. fragilis*). I must confess that I have not been able to corroborate this satisfactorily, owing probably to the fact that these cells frequently contain varnish-like golden-brown colouring matter, which gives a fictitious tint to their walls. It is possible, however, that these differences may become apparent after treatment with a suitable clearing reagent.

In *Populus* the periderm originates in the layer of cells immediately below the epidermis (*k.*, Fig. 2). It is only in *P. Fremonti* that I have noticed any departure from this rule (see Fig. 6, where the periderm has evidently originated in the third hypodermal layer), and even there it is of the nature of an irregularity, inasmuch as the normal condition is uniformly exhibited by the large majority of sections. Phelloderm is only formed after one or more rows of cork cells have been cut off. In Fig. 3 the first four rows of cells below the epidermis are cork cells; the narrow fifth row is, ostensibly, the meristematic layer or phellogen, in that it contains protoplasmic contents, and is limited by extremely thin tangential walls, while two cells on the left of the figure have just been cut off from it externally; the sixth row is the phelloderm. In *P. Fremonti* the layer which corresponds in position to the phellogen in other poplars always appears to convert itself into a layer of stone cells at the end of the season (*sc. l.*, Fig. 6). The succeeding season's

periderm, which originates from the phelloderm, if such it be, is terminated in the same way by a similar layer of stone cells, so that the periderm of an older piece of bark exhibits a more or less concentric series of sclerenchymatous layers (*sc. l.*, Fig. 7). The outer layers of the periderm, however, show a strong tendency to exfoliate, and the last-formed layer of stone cells is sometimes exposed.

The cork cells of young poplar twigs are nearly isodiametric, or somewhat elongated radially (*k.*, Figs. 2, 3, and 6), in older barks they usually present the customary flattened and tangentially elongated outline (*k.*, Figs. 5 and 8) ; the extent to which tangential elongation occurs may vary somewhat, however, even in the same section, and is generally least pronounced where the production of cork is vigorous. These periderms consist, with few exceptions, of thin-walled suberised cells : in *P. deltoides* and *P. pyramidalis* I have occasionally observed tangential bands of thickened cells (*sc.*, Fig. 8) and more examples of this could, doubtless, be found, especially in cases where the periderm is copiously developed ; but it is only in *P. Fremonti* that the regular formation of bands of thickened cells becomes (apparently) a fixed and constant feature.[1] In all these cases the thickened portions of such cells are, without exception, lignified, while the region of thickening extends uniformly around the whole cell ; the latter point is, nevertheless, subject to many fluctuations. The amount of phelloderm formed in *Populus* is always slight. With the one exception of *P. Fremonti*, the periderms of the poplars do not afford any characters of much diagnostic value, although the relative thicknesses of the periderms as a whole, in different species, may be of some importance in extreme cases : thus the covering of periderm in *P. tremuloides* and *P. grandidentata* (Figs. 28 and 30) is almost invariably thin, while in *P. angustifolia* and *P. pyramidalis* (Figs. 34 and 36) it is thick, sometimes excessively so.

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[1] It is, of course, possible that this peculiarity may be dependent upon ecological factors, and as I have only examined specimens from one locality (San Bernardino, S. California), the particulars of the latter, which were very kindly furnished by Mr. S. B. Parish, of S. Bernardino, Cal., are herewith appended :—" Specimens from a tree about 2½ ft. in diameter, about 40 ft. high, and not over thirty years old. Growing in loamy soil which is naturally somewhat damp, and contains a noticeable percentage of alkali, as indicated by the growth of *Distichlis maritima* and *Baccharis Emeryi*."

(2) Cortex.

The cortex in both genera exhibits a collenchymatous outer portion. This may vary, within certain limits, in the same species, it being frequently the case, for instance, that both the number of layers and the amount of thickening which they have undergone are relatively greater in the younger stages than in the older ones; any differences in this direction, therefore, must be interpreted with caution in comparing the barks of different species. With these reservations, then, it may be stated broadly that collenchyma, though not copiously produced, is more consistently and regularly present in the willows than in the poplars; among the latter its characters are not constant enough to be made use of, although some species show a stronger tendency towards collenchyma than others: thus the larger portion of the narrow cortex of *P. alba* is usually strongly collenchymatous, whereas in *P. Fremonti* there appears to be little collenchyma at any stage. The internal portion of the cortex consists of thin-walled cortical parenchyma of the usual type. Stone cells or groups of stone cells (*sc.*, Figs. 3, 5, and 24) are always to be found in the cortex of poplars—Moeller (p. 90) cites *P. nigra* as an exception, but this is incorrect—whereas stone cells have only been recorded from three species of *Salix*, viz.: *S. alba*, *S. fragilis* (von Höhnel, p. 93), and *S. Caprea* (Moeller, p. 90); von Höhnel specifically states that they are absent from *S. Caprea* (p. 93). I have so far been unable to find them in the specimens of *S. alba* and *S. Caprea* which I have examined, but it is very probable that they are present in the former species, seeing that they are common in the var. *vitellina*, where they appear to originate in the pericycle as well. In *S. fragilis* they are few and far between, and in the majority of sections they are not shown; it may be owing to this factor that an apparent contradiction occurs in some of Moeller's statements—he states on p. 95 that small groups of stone cells sometimes occur in the primary bark of *S. fragilis*, whereas on p. 90 he just as unequivocally maintains that *S. fragilis* forms no stone cells.[2] In all the other willow barks which I have examined, viz.: those of *S. aurita* × *Caprea*, *S. babylonica*, L., *S. cordata*, Muhl., *S. discolor*, Muhl., *S. fluviatilis*, Nuttall, *S. fragilis*, L., *S. hippophaifolia*, Thuill., *S. missouriensis*, Bebb, *S. nigra*, Marsh., *S. nigricans*,

[2] It is also possible that a transposition of names may have occurred on one of the pages, for it is further stated on p. 94 that sclerotised parenchymatous cells are entirely wanting in the bark of *S. Caprea*.

Sm., *S. pentandra*, L., *S. phylicifolia*, L., *S. purpurea*, L., *S. purpurea* var. *minor*, *S. rubra*, Huds., *S. triandra*, L., *S. viminalis*, L., *S. viridis*, Fries., and *S. Wardi*, Bebb, I have so far failed to detect any stone cells in the cortex (or in any other part of the bark). In *Populus* the quantity and grouping of the stone cells can be profitably utilised in differentiating the barks—their shape and size seem to possess but little diagnostic value—while the dimensions of the whole cortex are also of some importance, as will be shown presently. Wherever stone cells occur (whether in *Populus* or in *Salix*) they are always encrusted with prismatic crystals of calcium oxalate (*cryst.*, Figs. 3, 5, and 24). Sacs containing cluster crystals of calcium oxalate invariably occur in the cortex of both genera, but they are much more abundant in some species than in others; thus, in *S. viminalis* and *P. alba* (Fig. 29) they occur but sparingly, while in *S. alba* and *P. nigra* (Fig. 37) they are abundant. I have found starch present, in very small grains, in the cortex of some willows and poplars and absent in others, but, in view of the fact that the barks were collected at widely varying periods of the year, this point has not been pursued any further. *S. fragilis* and *P. canescens* are examples of barks in which abundant starch grains were seen, and *S. purpurea* and *P. angustifolia*, in which they were absent. It is evident, however, that the statement made by Moeller in his atlas[3] that willow bark never contains starch, requires modification.

(3) The Region of the Pericycle.

Dealing first with the pericyclic fibre-groups, we have Moeller's assertion (p. 91) that their fibres are remarkably small in comparison with those of the secondary bast. This observation appears to hold good in the case of the poplars, with few exceptions; actual measurement tends to show, however, that the difference is not, in many cases, as great as one might be led to believe. Figs. 16 and 17 (*b.f.*) exhibit the greatest extremes that I have seen (*P. tremuloides*). But in the twenty-three willows examined and enumerated above I have failed to confirm Moeller's statement in a single case: in the large majority of instances there is no appreciable difference in their size, but the fibres of the pericycle are slightly larger, if anything; in the few cases where there is a noticeable, although slight, difference—as in *S. missouriensis*

[3] 'Pharmacognostischer Atlas,' von Dr. J. Moeller, p. 282. Berlin 1892.

and *S. nigricans*, for example—the advantage is on the side of the pericyclic fibres. As it is important to be able to distinguish the pericyclic fibres from those of the secondary bast, it will be necessary to consider both of them here, although the consideration of the bast fibres belongs more properly to the next section. Both are usually polygonal in transverse section, but the pericyclic fibres frequently possess a tendency to become rounded at the corners and elongated in a tangential direction. In *Populus* the fibres of the bast never exhibit sharp striæ, whereas those of the pericycle generally do—compare Fig. 16 with Figs. 17, 19, 20, etc., on this point: the finer concentric lines which I have drawn in Fig. 18 are somewhat hypothetical, and were introduced mainly as shading; finding that they might tend to mislead, I have omitted them from all subsequent sketches. In *Salix*, in the large majority of cases, both sets of fibres exhibit very distinct striations; so very sharp, indeed, are these in many instances that they present the appearance of deep grooves formed by an etching needle. The striations are frequently finer and more numerous in the pericyclic than in the bast fibres, but exceptions occur which will be considered in detail later on. In both genera the fibres of the pericycle, with few exceptions, react much less strongly with phloroglucin and hydrochloric acid than those of the bast—a feature which usually affords a ready means of identification. The "middle lamella" is everywhere the most lignified part of the fibres, and is uniformly relatively thin in the bast fibres of the poplars, but subject to variations elsewhere. The groups of fibres in the bast are beset with sacs containing prismatic crystals of calcium oxalate, whereas these sacs usually occur but sparingly in connection with the groups of the pericycle. This factor is, no doubt, responsible to some extent for the darker appearance which a fibrous group of the bast presents after treatment with phloroglucin and hydrochloric acid, inasmuch as the crystals in the sacs are enclosed in an envelope—said by Pfitzer (de Bary, p. 140) and by Moeller (p. 92) to consist of cellulose (!)—which is very deeply stained by that reagent. By means of a combination of the above factors it is nearly always possible to distinguish the pericyclic fibres from those of the bast, for although one or more of these factors may not hold good in individual cases, the residue of them is usually ample to settle the question.

The groups of pericyclic fibres may or may not become broken up as the bark increases in thickness, but in the

poplars, at all events, their behaviour is too erratic to be of much diagnostic value (compare Figs. 37 and 38, both representing *P. nigra*). Where extensive tangential bands of stone cells arise in the pericycle, the splitting apart of the fibrous groups is nevertheless usually more pronounced than in those cases where such bands are feebly developed or not at all (compare, for example, Figs. 28 and 31 with Figs. 32 and 38). Large groups of pericyclic fibres are also more commonly to be found where the bast rays are wide and sharply delimited, as in *S. cordata* and *P. nigra*. As has already been hinted at above, stone cells occur in the pericycle; the extent to which they are developed and the nature of their distribution are factors of great importance in classifying the poplar barks. The fact that stone cells occur in the pericyclic region of *S. alba* var. *vitellina* has already been mentioned above; I have never seen stone cells internally to this in either of the two willows in which they were found by me.

In those parts where neither pericyclic fibres nor bands of stone cells occur it is not usually possible to distinguish the pericyclic region from the cortex on the one hand, or from the outer part of the medullary rays on the other; but barks in which the parenchymatous cells generally are filled with dense contents, commonly exhibit a connecting tangential band of cells, with more scanty contents than the others, between the pericyclic fibre groups. It is convenient in such a case to look upon these clearer bands as part of the pericycle.

(4) The Bast.

The separation of the bast into wedge-shaped bast rays and intervening widened medullary rays is very well shown in some barks (*S. cordata*, *S. nigra*, *P. tremula*, and *P. Fremonti*, for example), but in others the very reverse is the case (*S. purpurea*, *S. alba*, *P. canescens*, *P. pyramidalis*). It is interesting to note that de Bary (p. 536) took the willows—or, more exactly, "*S. fragilis* and allies"—as a type of the latter case, and ascribed the condition of affairs to uniform dilatation of the parenchyma. He states that if attention be directed to cases of extreme difference, it is found that in the one case[4] (the one just mentioned) dilatation of the entire parenchyma of the bast takes place in an approximately uniform proportion, as each annular zone becomes shifted outwards. In all the radial bands, and thus most clearly in the medullary rays of every degree, the parenchymatous cells increase uniformly,

[4] See also the figure in Planchon and Collin, p. 255.

and quite gradually in breadth, in the centrifugal direction. The intermediate non-equivalent tissues, which do not grow with them, especially sieve tubes and bast fibres, thus become uniformly removed one from another, and the more so the further they are from the cambium. In the other extreme case the dilatation is unequal in the various bands of the transverse section; it amounts to little or nothing in the bundles, and is most active, either in all the parenchymatous (= "medullary") rays or in some of them. Between the lateral limits of these dilated rays the arrangement and lateral distance from one another of all elements of the tissues remains approximately the same. Details are then given of *Tilia*, which is a typical case of this category, and which exhibits the resulting severance of the bast into wedge-shaped bast rays and medullary rays very distinctly; *Salix cordata*, however, would have illustrated the point almost as well, although the inner portions of the medullary rays are, unlike those of *Tilia*, only one cell thick, and no more. In addition to the above factors, displacement of the tissues, by stone cells in the case of some species of *Populus*, and by the distension of scattered parenchymatous cells in the case of *S. babylonica*, appears to play a part of some importance in preventing the formation of clearly defined wedge-shaped bast rays. Stone cells are invariably present in the bast of *Populus*; this has been denied by Moeller for *P. nigra* (pp. 90 and 93), but all the sections of the latter which I have examined contain them. Stone cells are always absent from the bast of *Salix*. The size and shape of the stone cells usually show differences as great among themselves in any one bark as they do from one bark to the other, so that they possess little diagnostic importance. *P. tremula*, however, exhibits some mature stone cells which possess thinner walls than in the other species; but even here the majority of them are furnished with very thick walls (*sc.*, Figs. 18 and 23), as in the other species (*sc.*, Figs. 17, 19, 20, 23, 25); their walls are always distinctly striated. In the larger cells these walls are frequently traversed by numerous branching pits (similar to those shown in the group of cortical sclerenchyma on the right of Fig. 24), while they are less abundant in the smaller ones; the converse, however, or anything between the two, is by no means rare (compare figures on Plates III. and IV.).

The amount and mode of grouping of these elements are, in contradistinction to their individual features, of the very greatest importance for comparative purposes, and will be fully dealt with below.

The medullary rays in both genera always consist of a single row of cells in the internal portion of the bark. In certain species of *Salix* (*S. alba, S. pentandra*) some of their cells are swollen out like bladders; this never seems to occur in the poplars. The cells of the medullary rays in this region usually show the customary radial elongation, and can thereby be readily identified (*S. nigra, P. alba*), but in some cases this is so little accentuated that their identification is rendered more difficult (*S. nigricans, P. pyramidalis*). Toward the exterior the medullary rays expand in very varying degrees and become many cells wide in the form with wedge-shaped bast rays. It is in these widened portions that stone cells are most constantly to be found in the poplars; it is to be noted in this connection that Moeller (p. 90) commits himself to the statement that the medullary rays do not become sclerotic in their passage through the clefts of the fibre plates.[5] It is reasonable to assume that the spaces between the fibre groups in the widened portions of the medullary rays are excluded in the definition, for Moeller's observation would otherwise be palpably inaccurate. Taking it for granted, therefore, that only the unexpanded portions of the medullary rays are referred to, it must be admitted that, even then, this contention is not justified by the facts, as Figs. 18 (*P. tremula*), 19, and 20 (*P. angustifolia*) clearly show. In the majority of instances, however, the medullary rays do not become sclerotised when in the single-rowed condition. It must be specially emphasised that nothing of all this applies to the willows, inasmuch as the latter never become sclerotised in any part whatsoever of the bast. Moeller's further statement that the medullary rays never take part in covering the bundles of fibres with crystals is also not quite correct, for I have occasionally observed prismatic crystals in this position in a number of species of *Populus* and *Salix* (see *cryst'*., Figs. 18, 19, 20, and 22).

With regard to the occurrence of calcium oxalate in other parts of the medullary rays, Moeller states that the medullary rays, generally, very seldom contain calcium oxalate. This holds good in the main, as far as the single-rowed parts of the rays are concerned, but clusters are sometimes to be found in them (*S. Caprea, P. tremula*); but, as soon as the medullary rays begin to divide, cluster crystals are, as a rule, more abundant in them than in any other portion of the bark

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[5] "Auch werden sie bei ihrem Durchtritt zwischen den Spalten der Faserplatten nicht sklerotisch."

(*S. Caprea*, *S. cordata*, *P. tremula*, *P. Fremonti*, compare also Figs. 28 to 39). As Moeller only recognises widenings of the medullary rays in one case, viz., that of *P. tremula*, it is not strange that he should omit to record the existence of calcium oxalate in them. Some of these expansions in *P. tremula* are, as Moeller states, of fusiform outline in transverse section; very good examples of these are also to be found in *P. alba* (Fig. 29), and occasionally in *P. grandidentata*. Such expansions are evidently only irregularities in the formation of the orthodox wedge-shaped bast rays, as may be seen by an inspection of a series of sections. Prismatic crystals are rare in the medullary rays (or any other part of the bark) unless accompanied by sclerenchyma of some kind. If an apparently isolated sac containing prismatic crystals be found, it is almost sure to prove, on further investigation, to consist of the borders of a mass of stone cells, or to be the prelude to the formation of sclerenchyma. *P. tremula*, which contains enormous sclerotic masses here and there (Fig. 32), illustrates the first point very well, as may be seen from Fig. 23, representing part of a medullary ray. In the upper portion of the crystal-containing area, shown in the figure, the stone cells, although omitted from the sketch, are easily seen in the actual section by focussing down, while one of the stone cells is shown at the bottom of the figure, projecting beyond the others. In the bast of the willows prismatic crystals are accordingly very rare, except in connection with the fibre-groups; such crystals, however, are present, according to von Höhnel (p. 92), in the bast of *S. amygdalina*, but I have not so far examined the bark of this species.

The bast fibres occur in groups of varying thicknesses, according to the species, and are usually arranged in tangential bands, interrupted by the medullary rays, and alternating with tangential bands of soft bast, which are likewise interrupted by the medullary rays. The tangential banding of the bast fibre groups in the willows rarely exhibits any serious irregularity, except suppression of groups. According to de Bary p. 527), a regular alternation of concentric zones of fibres and soft bast, of definite average breadth, takes place, within certain limits, in species of *Salix*. This appears to be correct in the majority of species, but in *S. aurita* × *Caprea*, *S. Caprea*, *S. babylonica*, *S. fragilis*, *S. discolor*, *S. cordata*, *S. nigricans*, and, to a less extent, in *S. rubra*, I have observed bands of soft bast, which occur at apparently regular intervals, and are usually more than twice as thick as the others; in these wider bands sieve tissue is

very copiously developed. In *Populus* I have not observed any peculiarities of this kind, but any deficiencies in this direction are more than amply compensated by decided eccentricities in other directions, and the irregularities which the configuration and distribution of the bast-fibre groups exhibit in such species as *P. tremula* and *P. Fremonti* far exceed anything occurring in the willows. In both genera the thickness of the fibre-groups and the extent to which they are suppressed are characters of good differential value (compare, for instance, *Salix viridis* and *P. nigra*, which have thin and frequently distant fibre groups, with *S. viminalis* and *P. tremuloides*, where the fibre groups are thick and rarely suppressed).

The soft bast is composed of bast parenchyma and sieve-tissue. The sieve tubes can be generally distinguished from the bast parenchyma by their larger size, their more scanty contents, their sharper angles, their tendency to collapse, and by the presence of sieve plates (*s.p.*, Fig. 26), which are compound and situated on very oblique walls (as may be readily verified in longitudinal section), so that their cross section—sometimes slightly oblique—is always seen in a transverse section of the bark, usually between two of the tangentially juxtaposed tubes. In a few cases, however, the difference in size between them and the parenchymatous cells is negligible (*P. Fremonti*, *S. alba*), while in *S. babylonica* the very much distended parenchymatous cells, which are distributed throughout the parenchymatous portions of the bark, exceed the sieve-tubes in size. There are other individual variations, especially in the poplars, but these will be considered later.

Crystal sacs occur in the soft bast of all the Salicaceæ, but the number present is very different according to the species; thus in *S. fragilis* and *P. pyramidalis* they are extremely abundant, but scarce in *P. alba*, and almost absent in *S. triandra*. These sacs contain cluster crystals, the presence of prismatic crystals being governed by the factors previously mentioned.[6]

Summarising now the points which are likely to be of use in distinguishing the poplar barks from those of the willows, we find that:—(1) The periderm of the willows is sharply differentiated from that of the poplars by the presence in the

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6 The observation made by de Bary (p. 530), but stated by him to require re-investigation, that both the cluster crystals and the prismatic crystals in *Salix* occur in the bundles exclusively, or to much the greater extent, is certainly not accurate in a large number of cases, as far as the cluster crystals are concerned, but this will be considered in greater detail later.

former, and by the absence in the latter, of cells which are thickened on the outer walls only, these thickened portions being suberised, but not lignified. (2) Stone cells are invariably present in the bast of the poplars, but always absent from that of the willows.

The pericyclic fibres in the poplars are, with a few exceptions, smaller than those of the bast. In the willows this is never the case. The bast fibres in *Populus* are also generally distinguished from those of *Salix* by their larger size and absence of evident striation, but neither of these characters affords such valuable evidence of identity as those mentioned above.

Systematic Examination of the Poplar Barks.

In this section the salient features of the barks examined, arranged in what is considered to be a fairly natural series, will first be described *seriatim*, and will be preceded, in each case, by a statement of the locality and date of collection (as far as known), and of the authority responsible for the determination. The whole will then be concluded by the construction of a key for the entire series.

Before proceeding to the descriptions, special attention is directed to the following conventional signs at the head of Plate I., as these are absolutely essential for a correct understanding of the figures :—

Cork or periderm is represented by crossed tangential and radial lines, the cortex and outer parts of medullary rays (and, incidentally, the parenchymatous portions of the pericycle) by a blank space, the pericyclic fibres by crossed diagonal lines, the bast fibres by slanted lines, the sieve-tissue and bast parenchyma by dots, the medullary rays by continuous radial or diverging dotted lines, the stone cells by black areas, and the cluster crystals of calcium oxalate by crosses.

Populus Tremuloides, Michx. (Fig. 28).—*Locality*, woods by Cascadilla Creek, just south of Dwyer's Dam, Ithaca, N.Y. ; collected on March 1, 1902 ; determined by Professor W. W. Rowlee, Cornell University, Ithaca, N.Y. Cork thin. Cortex rather narrow, with an occasional, usually small, group (up to 79μ in diameter) of stone cells. Collenchyma irregularly and not very copiously developed. Pericyclic fibre groups frequently accompanied by excessively thick bands (up to 223μ) of stone cells, and scantily provided with crystal-containing sacs; fibres never exceeding 26μ (average about 18μ), striated—one of the striations being

especially distinct (Fig. 16), and with a tendency to separate and become rounded, middle lamella slightly developed; parenchymatous portion of the pericycle usually with clear cells. The first layer of bast-fibre groups, in conjunction with stone cells that have usually arisen in the expanded parts of the medullary rays, forms a mixed sclerenchymatous ring with only distant and narrow parenchymatous breaks; the layer next to this internally subsequently behaves in a similar manner, and this process may be continued by the succeeding layers in older barks. The stone-cell aggregations in the first ring may attain as great a thickness as the pericyclic bands but the fibrous portion of the ring rarely exceeds 170μ. The rings internal to the first, in older barks, are rather thinner, and the fibre groups therein are very irregular in thickness, although they always preserve a strict tangential arrangement. The bast fibres (*b. f.*, Fig. 17) frequently exceed 26μ, and may attain 36μ, exhibit no evident striations, and present a pearly appearance and relatively slender middle lamella. Stone cells (*sc.*, Fig. 17) of every conceivable shape, thick-walled, and ranging from the size of the fibres to 78μ. Medullary rays distinct internally, but not towards the exterior, their one-rowed portions (in older barks than the one sketched) are occasionally lignified between the fibre groups, and may also contain prismatic crystals, but neither occurrence is common. Bast rays not clearly distinguishable externally, owing probably to total collapse of sieve tissue and dilatation of the bast parenchyma. Sieve tubes (*s. t.*, Fig. 26), quite commonly 28μ to 31μ across, apparently empty, elongated in a tangential direction as a rule, and usually juxtaposed tangentially. Bast parenchyma (*b. par.*, Fig. 26), very much smaller and with dense contents, forming thereby a striking contrast with the sieve tubes. Cluster crystals of calcium oxalate occur sparingly in the cortex and outer part of bast.

Note.—In a one-year-old twig there is a broken ring of small stone-cell groups in the outer part of the cortex, much as in Fig. 4 (*P. angustifolia*). The pericyclic fibres at this stage very rarely exceed 13μ.

Populus Alba, L. (Fig. 29).—*Locality*, Cambridge Botanic Garden; collected on July 23, 1901; determined at the Cambridge Botanic Garden. Cork of approximately the same thickness as the cortex. Cortex very narrow (from 5 to, unusually, 8 cells thick), and consisting mostly of collenchyma; nearly free from stone cells (but a broken ring of stone cells occurs in the one-year-old stem). Pericyclic fibre groups dis-

tant, frequently with small groups of stone cells adjoining them, the latter also occurring here and there in other parts of the pericycle; fibre groups scantily provided with crystal sacs. Pericyclic fibres very rarely exceeding, and seldom attaining, 16μ; middle lamella proper very thin and distinctly visible, "middle lamella" (=strongly lignified portion of outer walls) thick; one striation distinctly visible. The bast-fibre groups in the outermost layer form a nearly continuous mixed stone ring, as in *P. tremuloides*, and where small gaps still occur the cells are sclerotising (see *sclg.*, Fig. 25). The bands of stone cells may attain a thickness of 144μ, but may thin down to 79μ (or even 52μ) in the outer ring; or less, internally to it. Average thickness of fibre groups is fairly uniformly 79μ, but may be as little as 26μ, or as much as 117μ. Suppression of fibre groups may occur, and connecting bands of stone cells internal to the outermost ring are not formed so soon, as a rule. The bast fibres are of the same type as in *P. tremuloides*, but they do not usually exceed 26μ, although they may attain (but very rarely) 31μ; striations rarely suggested. Stone cells as in *P. tremuloides*, but tangential elongation is, perhaps, more frequent. Medullary rays distinct internally, but narrower than in *P. tremuloides* (compare *m.r.*, in Figs. 26 and 27), and fairly well marked externally; with fusiform local expansions; the one rowed portions occasionally lignified between the fibre groups. The bast rays, though not very sharp, are generally distinguishable throughout their course, owing to the fact that the sieve tubes retain their shape, more or less completely, for a considerable time. The sieve tubes (*s.t.*, Fig. 27) may attain a diameter of 39μ, and may possess scanty contents; they usually exhibit a nearly circular or polygonal outline, and only collapse slowly; sieve plates not distinct. Cells of bast parenchyma (*b. par.*, Fig. 27), of varying sizes, and with irregular and not copious contents. Cluster crystals of calcium oxalate occur but sparingly, and are very rare in the cortex proper and in the nner part of the bast.

Populus Grandidentata, Michx. (Fig. 30).—*Locality*, woods by Cascadilla Creek, just below Dwyer's Dam, Ithaca, N.Y.; collected on March 1, 1902; determined by Professor W. W. Rowlee, Cornell University, Ithaca, N.Y. Cork thin. Cortex wide, and invariably with abundant groups of stone cells (up to 260μ thick), which are commonly scattered, but sometimes occur in approximated tangential bands, the latter occasionally attaining 1·26 Mm. in a tangential direction; the stone cells themselves are usually, but by no means always, oval or

squarish, and do not commonly exceed 52μ (average, about two-thirds of this). Collenchyma feebly and scantily developed. Pericyclic fibre groups very white, isolated, or in mixed sclerotic bands, which may be as much as 1·8 Mm. wide in some cases; the stone-cell groups in these bands may attain a thickness of 117μ, and the fibrous portions are of approximately the same thickness—the average thickness of the whole bands is between 80μ and 100μ. Pericyclic fibres rarely exceed 14μ, and seldom attain them; striations generally absent; " middle lamella " very thick. A mixed continuous stone ring of very unequal thickness is almost invariably formed with the first band of fibres—there is, however, very occasionally, a break in this ring, which in one case observed attained a width of three parenchymatous cells—the stone-cell masses may here attain a thickness of 130μ, while the fibre groups beside them may be only 39μ thick, or may even get down to 26μ; in a word, the stone-cell groups are, as a rule, thicker than the fibre groups, but they may be thin, nevertheless (occasionally as little as 39μ); one of these stone-cell masses was seen which attained a thickness of 233μ in the radial direction, and stretched across two fibre bands, plugging up a medullary ray in a similar way to *P. tremula*. The bast fibres, which are seen to the best advantage in the more regular internal groups, sometimes attain 26μ, commonly 20μ, striations absent, appearance stony, middle lamina slender but sharp. The stone cells are of the usual type. Medullary rays not very distinct, the one-rowed portions with narrow cells much extended radially. Bast rays indistinct. Sieve tubes usually polygonal and nearly isodiametric, but otherwise approaching the *tremuloides* type in their tangential juxtaposition, their emptiness, and their recognisable sieve plates (although the latter are not nearly so distinct as in *P. tremuloides*); they attain, but seldom exceed, 26μ. The bast parenchyma is, for the most part, obviously smaller, and with dense contents. Cluster crystals scarce, but occurring throughout the bark.

Note.—In an older piece of bark, containing five layers of bast-fibre groups, the last-named may attain a thickness of 130μ. When the outermost continuous mixed ring shows signs of breaking up—as it occasionally does—the one next to it internally takes its place, as that has become a nearly continuous mixed ring also. There are local fusiform widenings in this older bark, but they are not so frequent as in *P. alba*; sclerotic bands frequently occur in such as are to be found, even between the inner fibre groups which have been separated by these widenings.

P. Canescens, Sm. (Fig. 31).—*Locality*, Royal Botanic Gardens, Kew; collected in March, 1901; determined at Kew. Cork fairly thick. Cortex very wide, collenchyma generally feebly developed, but fairly strong locally, especially when stone-cell groups, not far removed from the cork, occur below it. Stone cells very copiously developed (Fig. 24), in small or large groups, frequently scattered, but commonly approximated in tangential bands which may attain 3·25 Mm., and 210μ in thickness. Stone cells (Fig. 24) of very varying shapes and sizes (from 26μ to 105μ). Pericyclic fibre groups usually much broken up, and frequently forming mixed sclerenchymatous bands with stone-cell groups: the latter may be 105μ thick, or occasionally much more, for they are, at times, extremely irregular; the pericyclic groups themselves are seldom more than 65μ thick. The pericyclic fibre groups, when not involved with the stone cells, show few enveloping sacs with prismatic crystals, although more so than in most of the barks. Pericyclic fibres not usually exceeding 16μ, striations evident or not, "middle lamella" of varying thickness. The first layer of bast-fibre groups never forms a continuous mixed ring with stone cells, although bands, up to 1·45 Mm. in tangential direction, may occur. The thickness of the bast-fibre groups rarely attains 92μ, and seldom exceeds 65μ in the first layer; the groups internal to this, even in old barks, are thinner still, and rarely exceed 52μ. Such stone cells as occur in the bast are either mixed in with the bast fibres and not much wider—these are by no means abundant, and internally to the first layer they are distinctly rare—or else they occur in masses, up to 262μ in diameter, plugging up the medullary rays, or as irregularly distributed groups in the soft bast. Occasionally, also, the usual fill-up stone-cell group is found between two fibre groups in the wider part of a medullary ray (as far as this can be determined): the whole arrangement, in fact, is very irregular. Internally, suppression of the fibre groups is very common, some pieces of bark as large as the section drawn showing only about half the number exhibited in the one chosen. The secondary fibres may attain 26μ (quite commonly 24μ), have no obvious striations, and possess a moderately thick middle lamella. Medullary rays very narrow in the one-rowed portions and fairly distinct; both the medullary rays and the bast rays are confused towards the exterior. Soft bast enormously in excess and showing a distinct banding, caused by a regular alternation of bast parenchyma possessing dark granular contents with colourless and usually much collapsed sieve tissue. The

quantity of sieve tissue present is relatively very large. Sieve tubes up to 26μ, and of the *tremuloides* type on the whole, except that their mode of juxtaposition shows little regularity; their great abundance and their occurrence in tangential bands are, however, very striking features. The bast parenchyma is smaller, and with dense contents. Cluster crystals of calcium oxalate are extremely abundant everywhere except in the narrow parts of the medullary rays.

Note.—In a piece of older bark the inner bast conforms to what has been said above, but the fibre groups are extremely scarce, and hardly ever more than one fibre thick. The cork may be enormously thick, while in the cortex the formation of stone cells has hardly kept pace with the increase in tangential extension, and the cortex is, on the whole, less sclerotic, and there is, further, a tendency for the groups to get into line and to form a tangential band.

P. Tremula, L. (Fig. 32).—*Locality*, Cambridge Botanic Garden; collected on June 3, 1903; determined at the Cambridge Botanic Garden. Cork fairly thick. Cortex wide, collenchyma well developed on the whole, especially outside the stone-cell groups. Stone-cell groups always scattered, and of very varying size—from 79μ to 314μ or more (crossing the pericycle into the outer widened portion of a medullary ray in the latter case). The stone cells in these groups may be very thick-walled, as usual, or the walls may be rather thin. Pericyclic fibres generally in good-sized groups, the latter hardly ever in connection with stone cells, but always clearly at the apex of bast wedges, sacs with prismatic crystals of calcium oxalate fairly abundant on their outer surfaces, but scarce on their inner ones; the pericyclic fibre groups usually attain as great a thickness as the more developed of the bast-fibre groups, and, almost always, a greater tangential extension. The pericyclic fibres may attain 18μ, may be striated or not, and possess a moderately developed middle lamella. Bast-fibre groups, irregular in position and size, the latter factor varying, in the thickness, from 26μ to 118μ, and both these and intermediate sizes are common. The average size (as far as this can be determined) of the bast fibres is not very much greater than that of the pericyclic fibres, but it occasionally reaches 31μ, when the fibres are much extended in one direction; the bast fibres are not evidently striated, and possess a moderately thick middle lamella. The sclerotic groups are most frequently found in the outer parts of, or plugging up the medullary rays (Fig. 23); these masses may attain a radial diameter of 445μ.

Small groups of stone cells or single stone cells, are also found in the one-rowed parts of the medullary rays, between two bast-fibre groups, and projecting beyond the latter (*sc.* Fig. 18): this appears to be characteristic. A small group of stone cells is also occasionally affixed to one side of a fibre group in the usual way, but this is not common; and quite frequently the bast (and the cortex too) is, in some sections, almost free from stone cells, saving the narrow parts of the medullary rays, which are frequently lignified between the fibre groups. Bast rays and medullary rays extremely sharp; bast wedges rather erratic, but frequently broad and well shaped. Sieve-tubes hardly ever attaining 26μ until flattened in a tangential direction; intermediate, perhaps, between the *tremuloides* and *alba* types, but as they collapse early they are not of much descriptive value. Cells of the bast parenchyma frequently quite as large, and not easily distinguishable, at times, from the sieve tubes. Cluster crystals of calcium oxalate abundant, except in the inner part of the bast, where they may also be found in the one-rowed portions of the medullary rays.

P. Balsamifera, L. (Fig. 33).—*Locality*, side of road leading to Varna, Ithaca, N.Y.; collected on March 1, 1902; determined by Professor W. W. Rowlee, Cornell University, Ithaca, N.Y. Cork rather thin. Cortex fairly wide, with small groups (up to 262μ in tangential, and 52μ in radial direction) of stone cells few and far between in it. Collenchyma rather slightly developed. Pericyclic fibre groups distinct, up to 118μ thick, strikingly white, and almost free from juxtaposition with stone cells, although an occasional small group is seen; sacs with prismatic crystals of calcium oxalate scarce in connection with the fibre groups. The pericyclic band joining the fibres tangentially generally consists of clear cells. Pericyclic fibres rarely attaining 15μ, and, with a tendency to split apart, striations not obvious, except on borders of groups, middle lamella slender. The first layer of bast-fibre groups may form mixed bands with the stone cells, attaining a width, in some cases, of 1.26 Mm., and perhaps more; the fibrous portions of these attain 52μ in thickness, and the stone-cell groups a little more; such a band is then followed by a gap whose width may be as great as that of the band itself. The stone-cell groups usually occupy the normal positions in the widened portions of the medullary rays (as far as this can be determined). The second band from the pericycle, however, very closely approximates to the nearly continuous mixed ring condition which obtains in *P. tremuloides*. This ring may attain a thickness of

79μ (the average is not far from 65μ), and its regularity and evenness form a strong contrast to the two preceding types. The bast fibres may attain 26μ (average perhaps 18μ). Sieve tubes, bast parenchyma, and medullary rays of the *tremuloides* type. The sieve tubes attain, but rarely exceed, 26μ; they apparently collapse earlier than in *P. tremuloides*, and their sieve plates are not quite so distinct. Cluster crystals of calcium oxalate rather abundant in cortex, and sometimes in outer bast and medullary rays, but scarce internally to this.

Note.—Observations on older and younger barks show that the one-rowed portions of the medullary rays are always bold and wide, but the external portions are never very distinct. The fibrous layers in the inner portions of older barks are, as a rule, perfectly continuous (excepting the medullary rays, of course) and regular. Stone cells may occur occasionally in the fibre bands (or closely approximated to them) toward the exterior, but are comparatively rare. All mixed rings are broken at this stage.

P. Angustifolia, James (Fig. 34).—*Locality*, well-protected spot on Colorado College campus, growing in sandy soil; collected on March 14, 1902; determined by Mr. H. L. Shantz, Colorado College, Colorado Springs, Colo. Cork thick. Cortex rather wide; collenchyma feebly developed; stone-cell groups usually small (may attain a thickness of 131μ and a tangential extension of 262μ), and distantly arranged in a ring near the outside of the cortex for the most part; somewhat quadrangular or oval thick-walled cells, not generally exceeding 52μ, preponderate in these groups. Pericyclic fibre groups large (frequently 288μ in a tangential direction and 105μ thick, but occasionally more broken up) and seldom with stone cells abutting on, or tangentially in line with them; prismatic crystals of calcium oxalate in connection with them very rare. Pericyclic fibres attaining fully 26μ (average probably about 18μ), pearly, without evident striations, middle lamella relatively slender—characters generally associated with the bast fibres: they are, however, very white, and are only faintly stained by phloroglucin and hydrochloric acid. The tangential connecting bands of clear parenchymatous cells are frequently very striking. A mass of stone cells, attaining 288μ tangentially and 210μ radially in one mass measured, occasionally occurs in the widened part of a medullary ray just below the region of the pericycle, but this is quite rare. The first layer of bast-fibre groups is always feebly developed, and, although

stone-cell groups up to 131μ wide may occur in it, in the majority of cases the bast wedges are well marked off, owing to the absence of disturbing sclerotic groups; the fibre groups in this layer may attain 52μ in thickness. The second layer more nearly approximates to a continuous mixed ring, but frequent gaps occur, leaving the medullary rays unencumbered, and contributing to their distinctness; notwithstanding the fact that the stone-cell groups which occur here may attain a thickness of 65μ, whereas the fibrous groups seldom exceed 52μ, the banding presents a regular and orderly appearance. In addition to their occurrence in their normal positions, the stone cells are sometimes found in the bodies of the fibre groups, and also in the one-rowed parts of the medullary rays between two fibre groups, as shown in Figs. 19 and 20. The thickness of the soft bast between the pericyclic fibre groups and the first layer of bast-fibre groups averages from 183 to 235μ, and from 183 to 205μ between the first and the second layers, leaving but about a third of the thickness of the whole bark for the remaining closely-approximated layers. The latter are about 65μ thick on the average (soft bast about 79μ), and are very regular, the fibre groups being hardly ever suppressed. It is true that the fibre groups may now and then attain a thickness much above the average (up to 131μ), but this does not interfere with the great regularity of the tangential banding. The individual fibres answer to the description of the pericyclic fibres with the exception of their behaviour towards hydrochloric acid, while the fibre groups are beset with sacs containing prismatic crystals of calcium oxalate. The medullary rays are noticeable on account of the interesting crystallisations and lignifications which occur in their one-rowed portions (see Figs. 19, 20, and 22); these may occasionally be seen even between the fibre groups of the innermost fibrous layer. The stone cells which occur in these positions generally keep within the slit between the fibre groups, without projecting beyond them as is frequently the case in *P. tremula*; otherwise the medullary rays are well-marked, wide-celled, and with dark granular contents. Both the bast rays and the medullary rays are hence recognisable throughout, although the former sometimes lack sharpness in the outermost portion of the bast. Sieve tubes, bast parenchyma, and medullary rays of the *tremuloides* type, but bast parenchyma relatively large. The sieve tubes are frequently 26μ wide. Sacs containing cluster cystals of calcium oxalate are fairly abundant in the cortex and outer parts of the medullary rays, but scarce elsewhere.

Note.—In some sections the third layer of bast-fibre groups from the pericycle is feebly developed, giving, in places, the appearance of a wider band of soft bast.

P. Monilifera, Ait. (*P. deltoides* [*vel deltoidea*], Marsh.) (Fig. 35).—*Locality*, Cambridge Botanic Garden; collected on June 3, 1903; determined at the Cambridge Botanic Garden. Cork thick, occasionally exhibiting tangential bands of stone cells where abnormally developed locally. Cortex rather thin on the average (it is above the average in Fig. 35); collenchyma rather strongly developed; stone-cell groups small (attaining 210μ in a tangential, and 131μ in a radial direction), and scattered. Pericyclic fibre groups free; or with bands of stone cells abutting on them from the medullary rays below, but also occurring tangentially in line with them; the former groups may attain a thickness of 79μ, and the latter of 105μ, with a tangential extension of 183μ. The pericylic fibre groups stain deeply with phloroglucin and hydrochloric acid, but they are sparingly accompanied by sacs containing prismatic crystals of calcium oxalate. Pericyclic fibres rarely exceeding, or even attaining, 16μ; usually with a conspicuous middle stria; middle lamella slender. First layer of bast-fibre groups averaging about 52μ, not infrequently banded by means of stone-cell groups stretching across the rather ill-defined medullary rays in the usual way; such stone-cell groups, however, are rather fitful in their appearance, and these mixed bands, whose average thickness is about 52μ, are seldom of much extent. The fibrous layers internal to this do not certainly average more than half the thickness of the preceding, and fibre groups are frequently suppressed, as in *P. canescens*. It is rare to find groups of stone cells further inward than the second layer of fibre groups, but small masses scattered here and there occasionally occur. The bast fibres are of the usual type, and may occasionally attain 26μ (commonly 23μ), the average dimensions are probably about 18μ. The medullary rays are narrow in their one-rowed portions, and never very distinct at any part of their course; but towards the exterior, the irregular groups of stone cells and the crowded cluster crystals of calcium oxalate contribute, with other factors, to make a separation of bast rays and medullary rays a matter of impossibility. The general facies of the soft bast is much like that of *P. tremula*. The cells of the bast parenchyma are distinctly smaller than the sieve tubes, but they soon swell out to the same size as the latter, which collapse early. The sieve tubes frequently attain a diameter of 26μ; sacs containing cluster crystals of calcium

oxalate abundant in cortex and outer parts of medullary rays, which are almost black with them; also very abundant in the remainder of the bast, and not infrequently occurring in the narrow parts of the medullary rays.

P. Pyramidalis, Salisb. (*P. nigra*, var. *pyramidalis*, Spach; *P. italica*, Moench.), (Fig. 36).—*Locality*, Cambridge Botanic Garden; collected on July 23, 1901; determined at the Cambridge Botanic Garden. Cork thick, excessively developed locally, and frequently with tangential rows of stone cells in these local developments. Cortex fairly wide; collenchyma slightly developed; abundance, size, and distribution of stone cell groups much as in *P. deltoides*, but may occasionally attain an irregular tangential extension of 360μ, and a similarly irregular radial diameter of 180μ, but so slight a difference as this is of no importance, and the great majority of sclerotic groups are no larger than in *P. deltoides*. The pericyclic fibre groups are usually much broken up (a large size for a fibre group is 157μ wide by 65μ thick), and, as a rule, are tangentially in line with groups of stone cells of approximately the same thickness, and not infrequently in juxtaposition with them. Pericyclic fibres rarely exceeding 13μ (7 to 10μ common); one striation, at least, discernible; "middle lamella" usually thick, and thin middle lamella proper occasionally visible also: these fibres stain deeply with phloroglucin and hydrochloric acid. The average thickness (about 39μ) of the layers of bast-fibre groups is pretty nearly the same throughout the bark, although it may range from 16μ to 52μ. The first layer externally does not seem to show the preponderance in size over the others which appears to be general in *P. deltoides*. I have observed small groups of stone cells, up to 65μ thick, in the three outer layers; they are usually affixed to the bast-fibre groups in the usual way, but whether they arise in the widened medullary rays or not is difficult to determine. The tangential banding of the bast-fibre groups appears to be much more regular than in *P. deltoides*, suppression of fibre groups being less frequent than in the latter species, and the gaps do not often exceed 360μ in a tangential direction; these gaps, by-the-way, do not appear to be governed by the medullary rays, a fact which adds to the difficulty of recognising the outlines of the bast rays if such be present. The bast fibres very rarely attain 20μ, and seldom exceed 16μ; they are of the usual type, but striations are sometimes suggested. The medullary rays are irregular in their course and not easy to follow; the cells of which they are composed are narrow, and not much elongated

radially; they have, further, a tendency to become extended tangentially, and to mingle with the bast parenchyma. The bast rays are equally indefinite. The sieve tubes may rarely attain 29μ, and exceed the cells of the bast parenchyma in size; they approach the *tremuloides* type but tangential elongation is not adhered to, their greatest extension being frequently in a radial or oblique direction. They are subject to early distortion and collapse, and much exceed the parenchyma in amount. Cluster crystals of calcium oxalate are extremely abundant throughout the bark.[7]

Note.—From what has been said above, it will have been gathered that the greatest similarity exists between this bark and that of *P. deltoides.*[8] The differential characters which seem to possess some degree of constancy are:—(1) The greater relative thickness in *P. deltoides* of the first layer of bast fibre groups with respect to those internal to it, and the more frequent addition to it of stone-cell groups, and (2) the less frequent suppression of bast-fibre groups in *P. pyramidalis.*

P. Nigra, L. (Figs. 37 and 38).—*Locality*, Royal Botanic Gardens, Kew; collected in March, 1901; determined at Kew. Cork fairly thick. Cortex usually somewhat narrow, but rather variable in this respect; collenchyma fairly well developed; groups of stone cells are present, but they are not very abundant, and seldom exceed 180μ, although they may occasionally attain 235μ in a tangential direction; stone-cell groups are relatively less abundant in the older barks, inasmuch as their formation does not keep pace with the growth in extent of the cortex. The pericyclic fibre groups may be broken up (as in Fig. 37), or they may be intact and of considerable size (Fig. 38); the number of sacs with prismatic crystals occurring in connection with them is relatively small; they are, as a rule, entirely free from stone cells, but a group of the latter, usually smaller than they (and certainly always thinner than the larger ones), may be attached to them. The pericyclic fibres very rarely exceed 13μ, but may, nevertheless, occasionally attain 16μ;

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[7]The expression, "throughout the bark," which has been repeatedly used in connection with the distribution of cluster crystals of calcium oxalate, does not include the cork, which has been disregarded in the consideration of these bodies.

[8]I have used this name in preference to "*P. monilifera*" throughout the descriptions, as it (or its variant "*P. deltoidea*") is the one by which the tree is generally known. It is, of course, not within our present purpose to enter into the question of its merits or demerits from the standpoint of rigid botanical nomenclature.

striations not evident; middle lamella thin. The layers of bast-fibre groups usually show a very regular tangential banding (Fig. 38), although fibre groups may be suppressed here and there, especially in the younger barks (Fig. 31); they are always narrow, the average thickness being about 26μ (as in Fig. 21) and the extremes 39μ and 13μ (the thickness of a fibre). Occasionally a stone cell or two is found in the fibre groups (*sc.*, Fig. 21), but this is not at all common. The bast fibres are of the usual type, and rarely exceed 13μ, although they may attain 16μ, or even more. Scattered groups or bands of stone cells occur now and then in the widened portions of the medullary rays; the bands usually occur in connection with the first or second layers of bast-fibre groups, and may attain a thickness of as much as 78μ, but rarely exceed 52μ. Stone cells, however, are less abundant in this bark than in any of the others. The widened medullary rays and the bast wedges are distinctly marked off from each other externally. The one-celled portions of the widened medullary rays, but particularly those medullary rays which traverse the bast wedges and widen little, or not at all, are broad, distinct, and sharp; the cells of the unexpanded portions of the medullary rays, or all the cells of those medullary rays which do not expand, are markedly elongated radially. The bast wedges are wide as a rule, but not always; sieve tubes rarely attaining 26μ, and seldom over 23μ, of the *tremuloides* type, but relatively more numerous. The cells of the bast parenchyma, although less numerous than in *P. tremuloides*, are relatively larger; cluster crystals of calcium oxalate abundant, more especially in the outer parts of the bark.

P. Fremonti, S. Wats. (Fig. 39).—*Locality*, loamy, somewhat damp soil, San Bernardino, Southern California; collected on February 24, 1902; determined by Mr. S. B. Parish, San Bernardino, Cal. Cork thin, characterised by the presence of concentric rows of stone cells at more or less regular intervals which induce exfoliation of its outer layers. Cortex usually wide, but somewhat irregular; collenchyma little developed; stone-cell groups irregular, rather numerous, scattered, and frequently of considerable size, attaining 270μ in any direction. Pericyclic fibre groups usually small and free, but with an occasional, generally smaller, group of stone cells abutting laterally upon them; they are only sparingly accompanied by sacs with prismatic crystals of calcium oxalate. Pericyclic fibres rarely exceeding 16μ, apparently not striated, and with a thin middle lamella. The external bast-fibre groups are clearly

limited to the very distinct bast rays, and are usually rather thick (about 78μ on the average), and irregular in their distribution; the inner groups are more regularly arranged, and tangential banding is general, although the bands are generally crooked. Bast fibres of the usual type, sometimes attaining 26μ, and commonly 23μ. Masses of stone cells occur here and there in the widened outer parts of the medullary rays, but these hardly ever show any tendency to unite with the bast-fibre groups. The medullary rays are distinct, numerous, and with notably wide cells throughout, which are radially elongated in their one-rowed portions. Bast rays very sharply delimited, owing to the relatively small size of their cells; clearly wedge-shaped, though irregular. Sieve tubes very rarely more than 20μ in their widest parts and nearly always radially juxtaposed; they are not appreciably larger than much of the bast parenchyma, and there is a tendency towards an arrangement of both sieve tubes and parenchymatous cells in radial rows. Cluster crystals of calcium oxalate are abundant in most regions of the bark, as a rule, but their distribution is at times erratic and local; they are commonly most abundant near the outer margin of the medullary rays and bast wedges.

Note.—This bark should probably have been placed somewhere near *P. tremula*, but the constant presence of thickened rows of cells in the periderm tempted me to place it as near the willows as possible, that is to say, at the least sclerenchymatous end of the series.

It now remains to construct a key for the series of barks above described, and the chart on the next page is an attempt in this direction.

In conclusion, I desire to express my very hearty thanks to the following gentlemen who have taken great pains to supply suitable authentic material for this investigation:—Professor I. B. Balfour, F.R.S., Regius Keeper of the Royal Botanic Garden, Edinburgh; Mr. B. F. Bush, Courtney, Mo., U.S.A.; Mr. Frederick V. Coville, Chief of the Division of Botany, United States Department of Agriculture, Washington, D.C.; Mr. E. M. Holmes, F.L.S., Curator of the Museums of the Pharmaceutical Society of Great Britain; the Director, Royal Botanic Gardens, Kew; Mr. R. Irwin Lynch, A.L.S., Curator of the Cambridge Botanic Garden; Mr. S. B. Parish, San Bernardino, Cal., U.S.A.; Professor W. W. Rowlee, Cornell University, Ithaca, N.Y., U.S.A.; Mr. H. L. Shantz, Colorado College, Colorado Springs, Colo., U.S.A.; and Professor William Trelease, Sc.D., Director of the Missouri Botanical Garden, St. Louis, Mo., U.S.A.

Salicaceae.

- **Populus.** Stone cells invariably present in the bast. Periderm never possessing cells whose walls are thickened on the outer side only, these thickenings being suberised, but not lignified.
  - Forms in which layers of bast-fibre groups form nearly continuous mixed rings with stone-cell groups in the first or second layers from the pericycle; and with few crystals of calcium oxalate in the inner part of the bast.
    - Extensive mixed sclerenchymatous bands in the pericycle.
      - Narrow cortex with little sclerenchyma. *P. tremuloides.*
      - Wide cortex with much sclerenchyma. *P. grandidentata.*
    - Mixed sclerenchymatous bands in pericycle rarely developed.
      - Outermost layer of bast-fibre groups combining to form a nearly continuous mixed ring with stone cells. Cluster crystals rare in cortex. *P. alba.*
      - Outermost layer of bast-fibre groups never combining to form a nearly continuous mixed ring with stone cells. Cluster crystals abundant in cortex. *P. balsamifera.*
  - Forms in which nearly continuous mixed sclerenchymatous rings in either of the two outer layers of bast-fibre groups and paucity of cluster crystals in inner portion of bast do not occur together.
    - Stone cells in abnormal positions. Medullary rays and bast rays very sharply marked off, and cluster crystals fairly abundant in inner parts of bast rays.
      - Concentric rows of stone cells present in cork. No abnormal sclerotic developments in the medullary rays. *P. Fremonti.*
      - No concentric rows of stone cells in cork. Medullary rays abnormally sclerotised. *P. tremula.*
    - Stone cells in abnormal positions, sharp bast and medullary rays and fairly abundant cluster crystals in inner parts of bast rays do not occur together.
      - One-rowed portions of medullary rays broad and distinct.
        - Groups of bast fibres in closely approximated bands internally. Groups commonly 65μ thick. *P. angustifolia.*
        - Groups of bast fibres not uncommonly suppressed internally. Groups rarely over 40μ thick, usually about 21μ. *P. nigra.*
      - One-rowed portions of medullary rays narrow or indistinct.
        - Cortex excessively sclerotic, bands may attain a tangential extension of 3·25 Mm., and a thickness of 210μ. *P canescens.*
        - Cortex only moderately sclerotic, aggregations of stone cells not above 200μ in tangential direction and 105μ in thickness.
          - First layer of bast-fibre groups usually twice the size of those internal to it. Suppression of bast-fibre groups extensive. *P. deltoides (P. monilifera, Ait.)*
          - First layer of bast-fibre groups not normally much exceeding in size those internal to it. Tangential banding of fibrous layers well marked. *P. pyramidalis*
- **Salix.** Stone cells invariably absent from the bast. Periderm always possessing cells whose walls are thickened on the outer side only, these thickenings being suberised, but not lignified.

Explanation of Figures.

Note.—All the sections are *transverse* sections.

PLATE I.

FIG. 1.—Section through epidermis and outer portion of cortex of first year's twig of *P. alba*; *h.*, hairs; *ep.*, epidermis; *coll.*, collenchyma. × 200 diameters.

FIG. 2.—Section through a somewhat older twig of same; *k.*, periderm or cork. Other lettering as before. × 200 diameters.

FIG. 3.—Section through outer part of bark of a one-year-old twig of *P. angustifolia* (that shown in Fig. 4); *cort.*, outer portion of cortex; *sc.*, stone cells; *cryst.*, prismatic crystals of calcium oxalate. Other lettering as before. × 200 diameters.

FIG. 4.—Section through a one-year-old twig of *P. angustifolia*; *x.*, wood; *m.*, pith. For explanation of other structures see conventional signs. × 30 diameters.

PLATE II.

FIG. 5.—Section through periderm and outer part of cortex of older bark of *P. angustifolia*. Lettering as before. × 200 diameters.

FIG. 6.—Section through a one-year-old twig of *P. Fremonti*; *hyp.*, hypoderma; *sc.l.*, sclerenchymatous layer limiting cork internally. Other lettering as before. × 200 diameters.

FIG. 7.—Section through periderm and outer portion of cortex of older bark of same; *sc.l.*, concentric sclerenchymatous layers in periderm. Other lettering as before. × 75 diameters.

Fig. 8.—Section through a copiously developed periderm of *P. deltoides*; *sc.*, tangential bands of stone cells in the periderm. Other lettering as before. × 200 diameters.

Fig. 9.—Section through outer part of bark of a two-year-old twig of *S. Wardi*; *k.*, outer bark, consisting largely of cork; *m.r.*, medullary ray; *b.r.*, bast ray. Other lettering as before. For structures not lettered see conventional signs on Plate I. × 75 diameters.

Fig. 10.—Section through outer part of bark of *S. alba*. Lettering as before. × 200 diameters.

Fig. 11.—Section through outer part of bark of a one-year-old twig of *S. Wardi*. Lettering as before. × 200 diameters.

Fig. 12.—Section through outer part of an older bark of *S. purpurea*. Lettering as before. × 200 diameters.

Fig. 13.—Section through outer part of bark of a first year's twig of *S. viminalis*. Lettering as before. × 200 diameters.

Fig. 14.—Section through different part of the same twig. Lettering as before. × 200 diameters.

Fig. 15.—Section through outer part of older bark of same species. Lettering as before. × 200 diameters.

PLATE III.

Fig. 16.—Pericyclic fibres of *P. tremuloides*. × 300 diameters.

Fig. 17.—Section through portion of mixed sclerenchymatous ring of *P. tremuloides*; *b.f.*, bast fibres. Other lettering as before. × 300 diameters.

Fig. 18.—Section through portion of bast of *P. tremula*, showing abnormal development of sclerenchyma (*sc.*); *cryst'.*, prismatic crystals of calcium oxalate in medullary ray; *clust.*, cluster crystal of calcium oxalate. × 380 diameters.

Figs. 19 and 20.—Sections through lignified parts of medullary rays between fibre groups in *P. angustifolia*. Lettering as before. × 380 diameters.

Fig. 21.—Section through bast-fibre groups enclosing stone cells in *P. nigra*. Lettering as before. × 380 diameters.

PLATE IV.

FIG. 22.—Section through part of medullary ray of *P. angustifolia*, provided with prismatic crystals of calcium oxalate between two bast-fibre groups. Lettering as before. × 380 diameters.

FIG. 23.—Section through a sclerotic mass from a medullary ray of *P. tremula*. Lettering as before. × 380 diameters.

FIG. 24.—Section through portion of a stone-cell group from the cortex of *P. canescens*. Lettering as before. × 380 diameters.

FIG. 25.—Section through part of bast of *P. alba*, showing cells in the process of becoming sclerotised (*sclg.*). Other lettering as before. × 380 diameters.

PLATE V.

FIG. 26.—Section through portion of soft bast of *P. tremuloides*; *s.t.*, sieve tubes; *s.p.*, sieve plate; *s.w.*, partition between adjoining sieve tubes not showing sieve plate; *b.par.*, bast parenchyma. Other lettering as before. × 380 diameters.

FIG. 27.—Section through portion of soft bast of *P. alba*. Lettering as before. × 500 diameters.

FIG. 28.—Section through bark of *P. tremuloides*. × 28 diameters. Conventionalised. For explanation see Plate I

FIG. 29.—Section through bark of *P. alba*. × 28 diameters. Conventionalised as before.

FIG. 30.—Section through bark of *P. grandidentata*. × 28 diameters. Conventionalised as before.

FIG. 31.—Section through bark of *P. canescens*. × 28 diameters. Conventionalised as before.

PLATE VI.

Fig. 32.—Section through bark of *P. tremula.* × 28 diameters. Conventionalised as before.

Fig. 33.—Section through bark of *P. balsamifera.* × 28 diameters. Conventionalised as before.

Fig. 34.—Section through bark of *P. angustifolia.* × 28 diameters. Conventionalised as before.

Fig. 35.—Section through bark of *P. deltoides* (*P. monilifera*, Ait.) × 28 diameters. Conventionalised as before.

Fig. 36.—Section through bark of *P. pyramidalis.* × 28 diameters. Conventionalised as before.

Fig. 37.—Section through bark of *P. nigra.* × 28 diameters. Conventionalised as before.

Fig. 38.—Section through older bark of same. Cluster crystals of calcium oxalate not shown. × 28 diameters. Conventionalised as before.

Fig. 39.—Section through bark of *P. Fremonti.* × 28 diameters. The darkest lines in the cork are the rows of stone cells, otherwise conventionalised as before.

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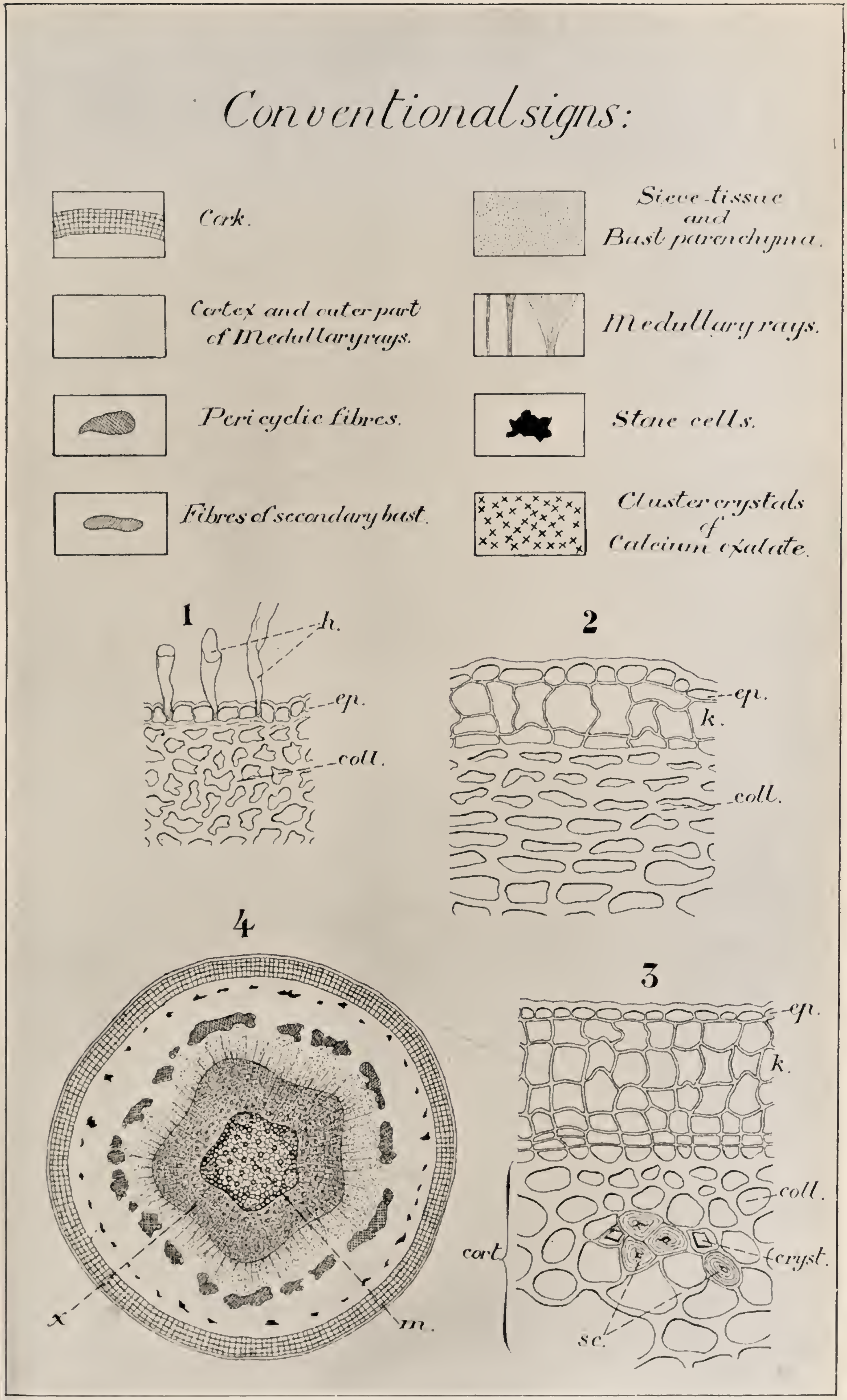
Conventional signs:
Cork.
Sieve-tissue and Bast parenchyma.
Cortex and outer part of Medullary rays.
Medullary rays.
Pericyclic fibres.
Stone cells.
Fibres of secondary bast.
Cluster crystals of Calcium oxalate.
1
h.
ep.
coll.
2
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k.
coll.
4
x
m.
3
ep.
k.
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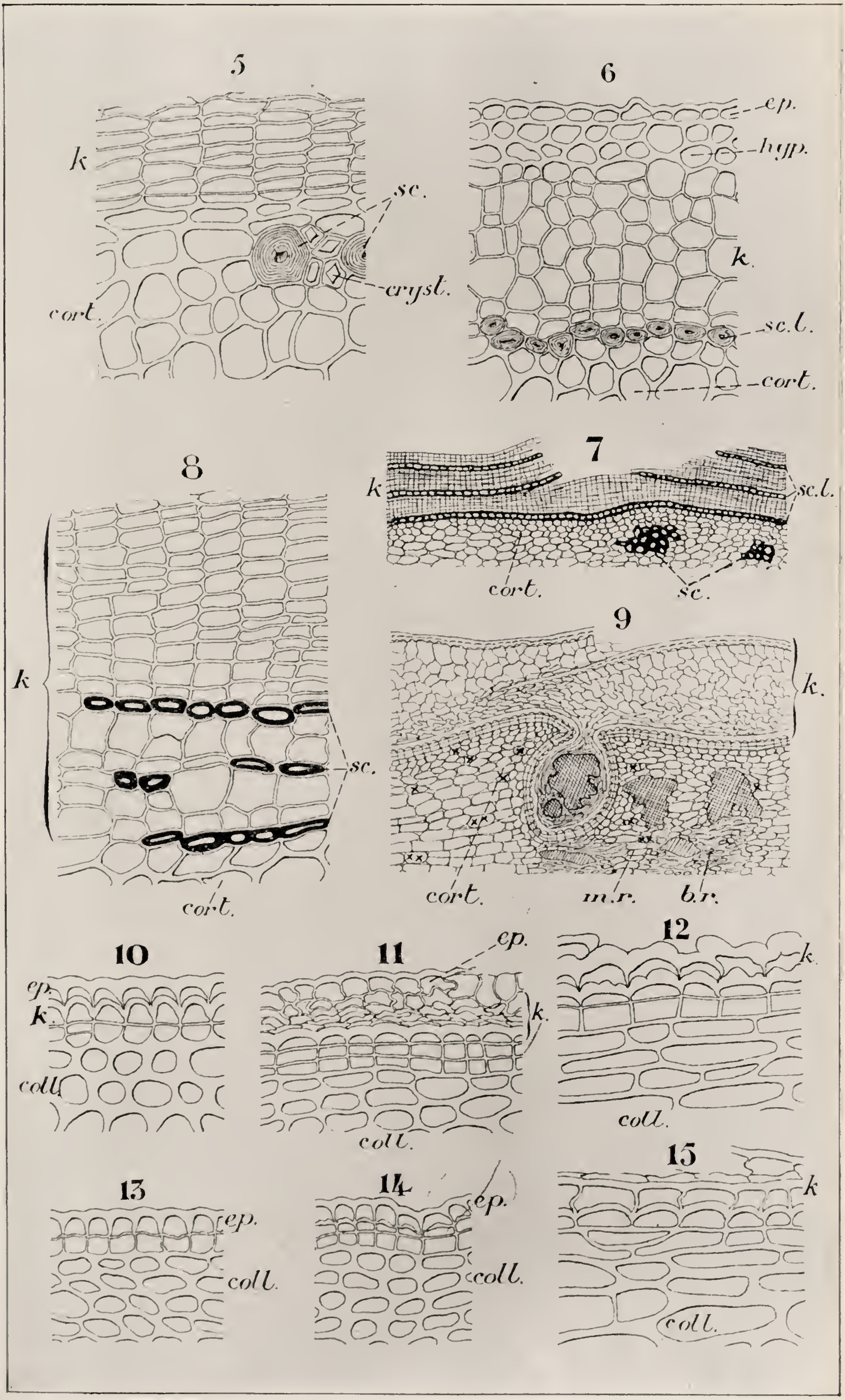
cort.
cryst.
sc.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k
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k
sc.l.
cort.
sc.
9
k.
cort.
m.r.
b.r.
10
ep.
k.
coll.
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14
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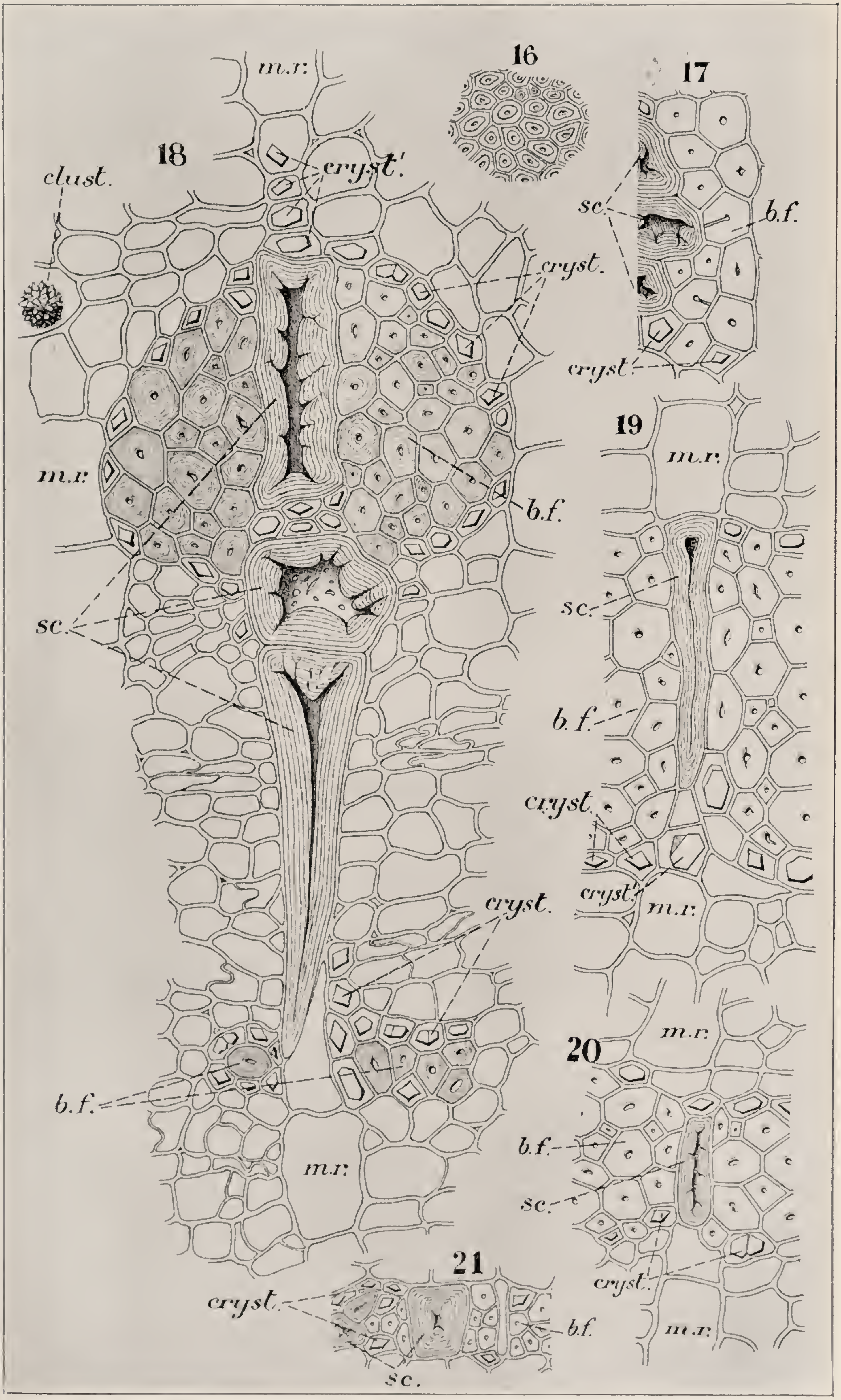
15
k
coll.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17
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m.r.
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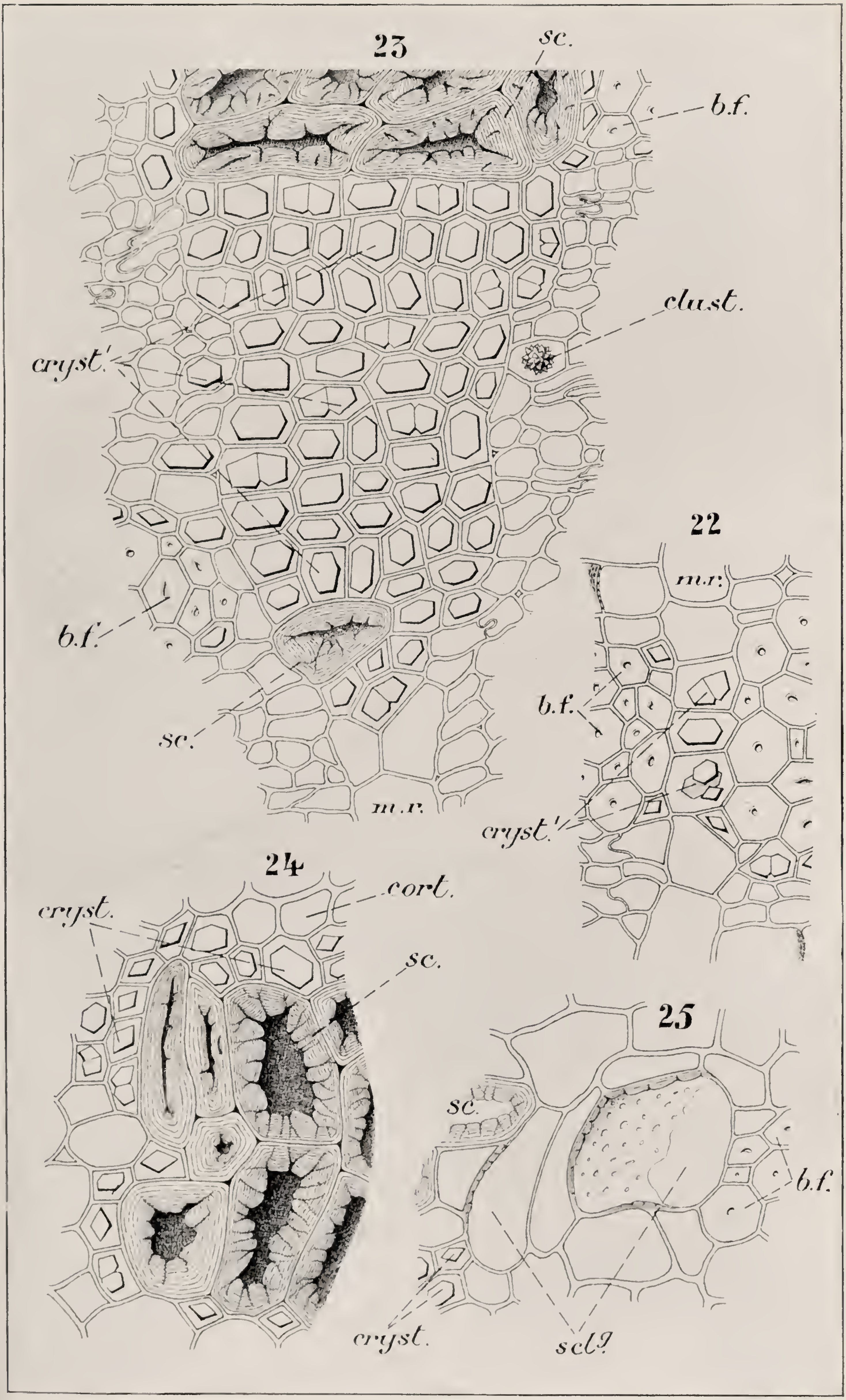
sc.
b.f.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sc.
b.f.
clust.
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m.r.
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cryst.
cort.
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25
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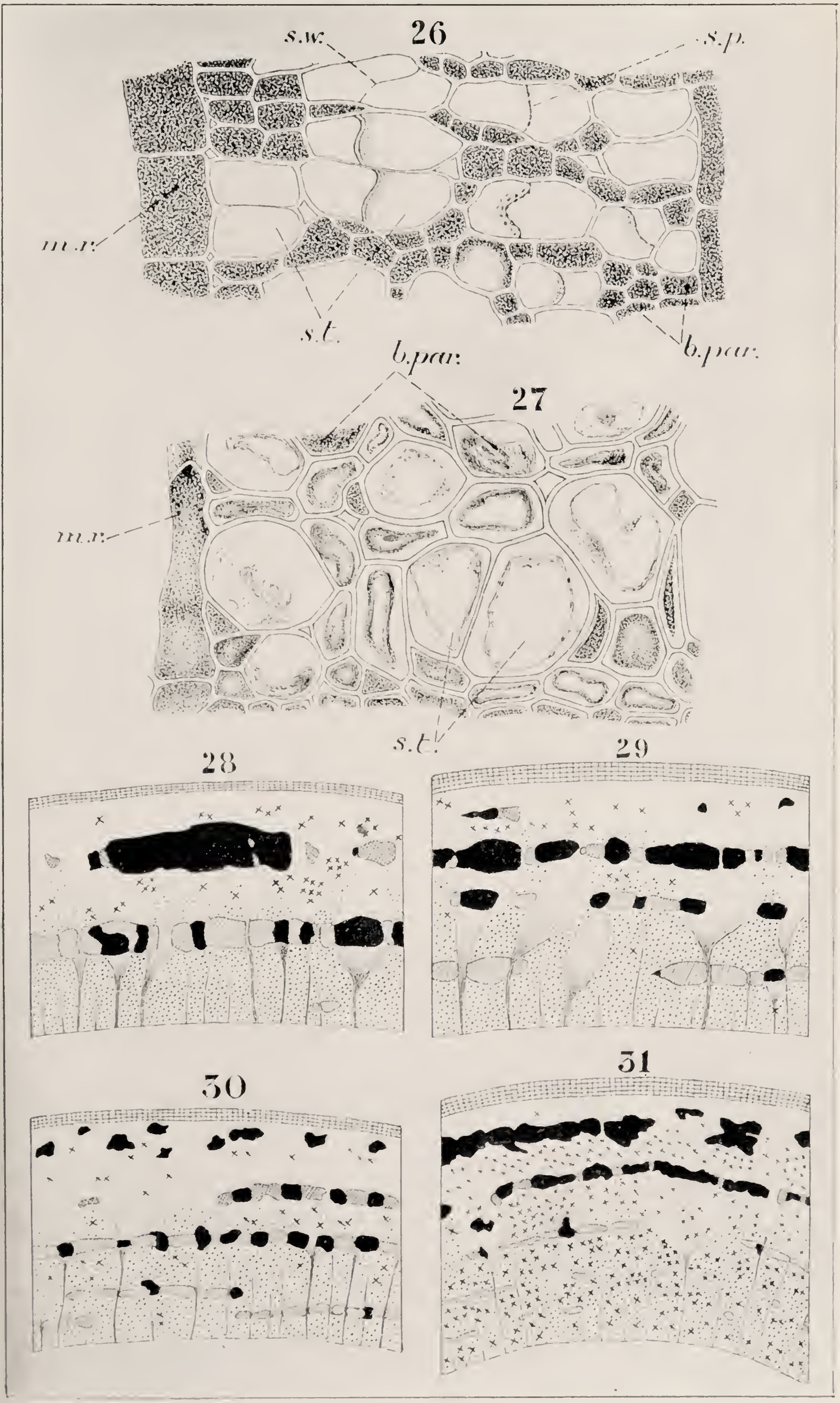
scl?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s.p.
m.r.
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s.t.
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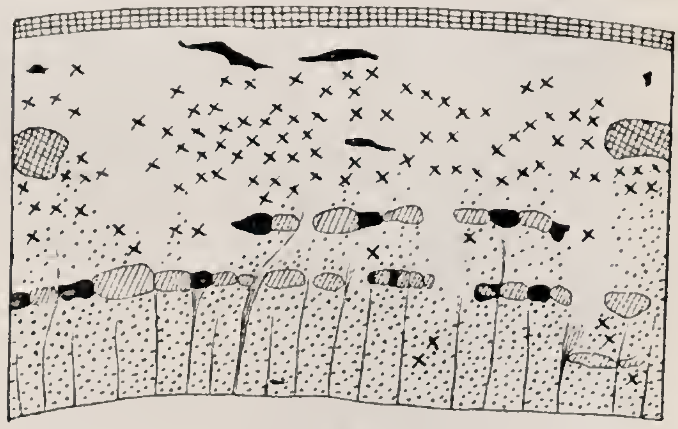

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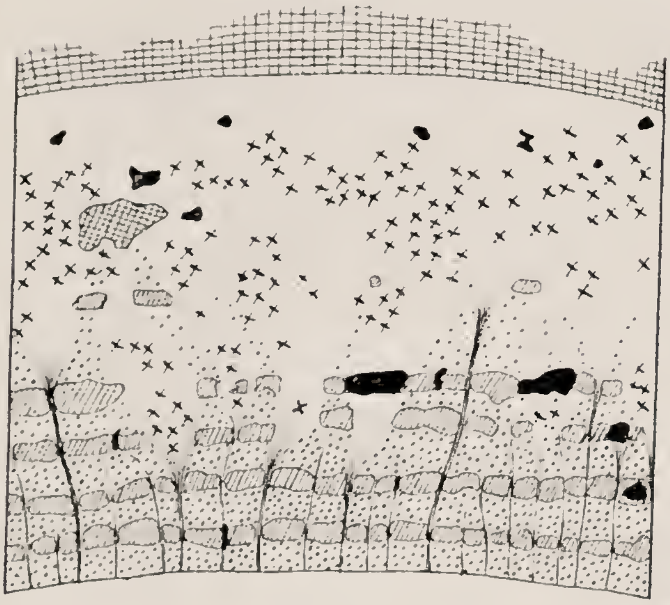

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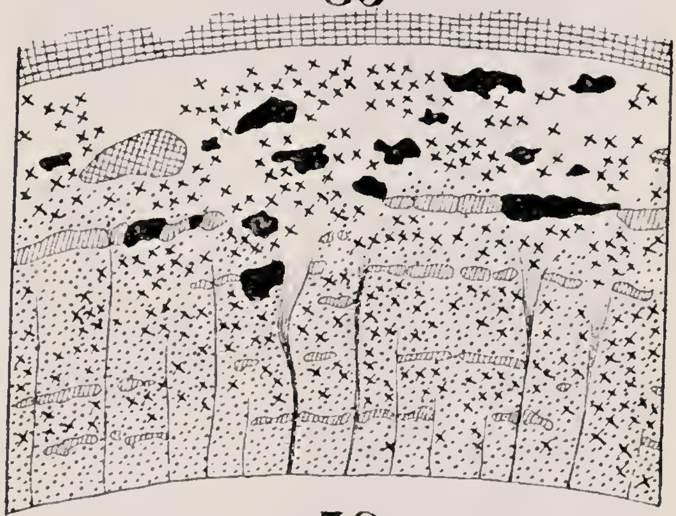

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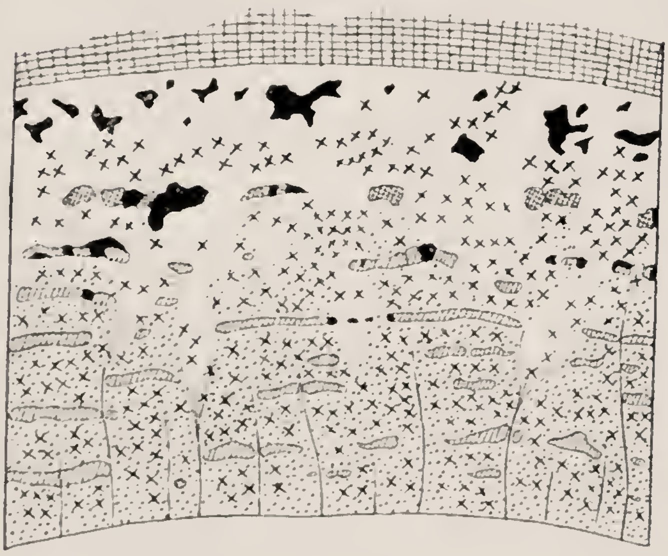

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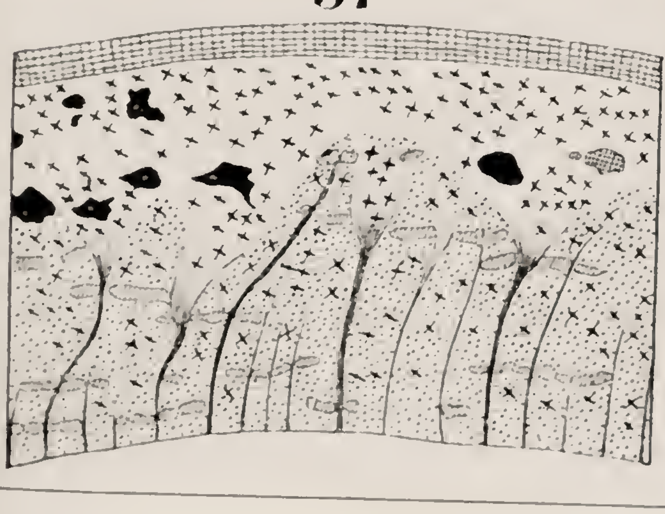

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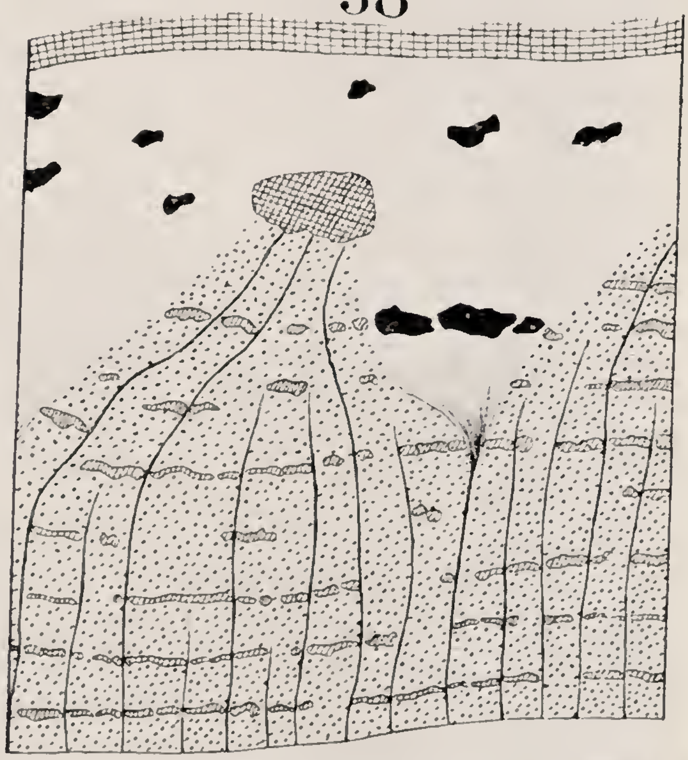

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